Limnologica 33, 77–91 (2003)
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LIMNOLOGICA

Seasonal dynamics of algal biomass and allochthonous input of coarse particulate organic matter in a low-order sandstone stream (Weidlingbach, Lower Austria)

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Received October 24, 2002 · Accepted February 4, 2003

Abstract

From December 1997 to December 1998, benthic algal biomass and the input of allochthonous coarse particulate organic matter (CPOM) were investigated in bi-weekly intervals at two sampling stations (shaded and sunny) of the Weidlingbach, a fourth order sandstone stream in the Wienerwald. A total of 41 benthic algal taxa was collected, belonging to the groups Cyanobacteria (4 taxa), Bacillariophyceae (33), Rhodophyta (1), Chrysophyceae (1) and Chlorophyta (2). At the shaded site, periphyton dry mass ranged from 13 g m^{-2} in April to 440 g m^{-2} in August (annual mean = 93 g m^{-2}), at the sunny site from 3 g m^{-2} in May to 512 g m^{-2} in late fall (annual mean = 70 g m^{-2}). Based on the algal carotenoid pattern, Bacillariophyceae were most abundant in fall and winter while Chlorophyceae dominated during summer. Mean annual standing stock of chlorophyll-a was 8.65 µg cm^{-2} at the shaded station and 7.53 µg cm^{-2} at the sunny site. Annual allochthonous CPOM input rates ranged from 382 to 665 g dry mass m^{-2} for aerial input and from 1006 to 1062 g DM m^{-1} of stream length for lateral input. Lateral input rates were influenced by the bank inclination; the temporal distribution of aerial input showed an autumnal maximum (61-65% of the total). Direct CPOM input was significantly highest ($P < 0.05$) during the period of defoliation from October to November. In the course of this period, 61.1% (shaded) to 64.9% (sunny) of the annual CPOM dropped into the brook, yielding daily input rates of 6.6 to 4.0 g DM m^{-2}. From December to September, daily direct input rates decreased to 0.84 g DM m^{-2} (shaded) and 0.44 g DM m^{-2} (sunny). At both sites, retention capacity was high; 70% of marked leaves released along transects were retained by coarse sediment particles within 40 m from the starting point. The annual mean of periphyton dry mass made up 52% of CPOM standing stock at the shaded site and 39% at the sunny site.

Key words: Algae – periphyton – pigments – CPOM – forest stream

Introduction

In temperate regions, streamside terrestrial vegetation influences river ecosystems in many ways, a key issue being the shift from allochthonous to autochthonous energy input along a stream as formulated in the well-known River Continuum Concept. As river width increases, coarse particulate organic matter (CPOM) input originating from terrestrial vegetation decreases (Vannote et al. 1980; Gurtz et al. 1988). Rounick & Win-

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TERBOURN (1983), CONNERS & NAIMAN (1984), GURTZ et al. (1988), BENFIELD et al. (1991), REED et al. (1994), MOLLA et al. (1996), GAYTE & FONTVIEILLE (1997) and ABELHO & GRAÇA (1998) demonstrated that distinct correlations exist between allochthonous and autochthonous input. Especially in autumn, huge amounts of CPOM are transferred from terrestrial vegetation into stream ecosystems (VANNOTE et al. 1980; STOCK & WARD 1989; DELONG & BRUSVEN 1993; FINDLAY et al. 1993; ROUT & GAUR 1994; WEIGELHOFER & WARINGER 1994). Upstream biocoenoses are frequently based on CPOM as the main energy resource, whereas autochthonous production is little there. The composition and density of the tree canopy strongly influence the quality and quantity of CPOM input (BÄRLOCHER 1983; CONNERS & NAIMAN 1984; CUSHING 1988; RICHARDSON 1992; WEBSTER et al. 1994; ALLAN 1995; JOHNSON & COVICH 1997; POZO et al. 1997; ABELHO & GRAÇA 1998). Because of high allochthonous organic input and only low autochthonous primary production, these sections can be addressed as heterotrophic systems (VANNOTE et al. 1980; LOCK et al. 1984; FRIBERG & KJELDSEN 1994; ROSEMOND 1994; ALLAN 1995). However, periphyton may nevertheless form an important food source of micro- and macroinvertebrates (ROUNICK et al. 1982; ROUNICK & WINTERBOURN 1983; WINTERBOURN et al. 1985; MAYER & LIKENS 1987; HILL & KNIGHT 1988).

One reason for little autochthonous production is riparian shading which may reduce the incoming radiation down to 5%, thus leading to heavy light limitation of benthic primary producers (GURTZ et al. 1988; HEPINSTALL & FULLER 1994; HILL et al. 1995; HILL 1996; POZO et al. 1997; WEBSTER & MEYER 1997; SCHAGERL & DONABAUM 1998; KJELDSEN et al. 1998; HILL & KNIGHT 1998).

The present study at the Weidlingbach addresses the issues described above and explores the poorly-known relationship between seasonal dynamics of algal biomass and allochthonous input of CPOM by comparing a sunny and a shaded site throughout one year. Furthermore, the retention capacity was investigated at the two sites.

Study area

The study was carried out at the Weidlingbach, a 12-km-long, first to fourth order tributary of the Danube. Its drainage area (33.2 km^2) is situated in the Wienerwald, the densely forested easternmost spur of the Alps near Vienna, Austria (Fig. 1; 48°17′ N, 15°16′ E; altitude of source: 440 m; altitude of mouth: 164 m above sea level). Near the source, mean stream width is 2.1 m and maximum water depth 16 cm, near the mouth 3.9 m and 71 cm, respectively. The chemical properties of the water are heavily influenced by the calcareous sandstone, marl and slate geology, producing relatively high conductivity (480–1100 µS cm^{-1}) and total hardness (up to 12 mval l^{-1}). Annual pH values range from 6.6 to 8.4, and dissolved oxygen is always above 80% saturation. The range of annual water temperatures is 0.0–18.0 °C at the first order and 0.5–20.0 °C at the fourth order sections of the stream (LANG et al. 2001). At the third order study area, water temperature ranged from 0 °C in late fall to 19 °C in mid-summer.

The catchment is covered mainly by deciduous forest consisting of *Fagus sylvatica* L., *Carpinus betulus* L., *Quercus* spp. and *Acer* spp.; lower reaches of the stream are bordered by human settlements. Sandy substrates are common within first and second order tributaries, but cobbles and pebbles predominate in the lower reaches. The mean annual discharge of first order tributaries is 2 l s^{-1}; near the mouth it rises to 200 l s^{-1}. During spates the discharge may be as high as 7200 l s^{-1} due to the poor infiltration capacity of the soil (HADL et al. 1976). During the investigation period, the water level was highest in spring and early summer due to snowmelt and precipitation.

The two sampling sites were situated approximately 7 km from the mouth and separated by a 200-m-long stream section. Site 1 was 16.6 m long and 9.1–9.4 m wide with an inclination of 35–40° at both banks. The stream bed was completely shaded by trees (*Acer campestre* L., *A. pseudoplatanus* L., *Alnus glutinosa* (L.) GAERTN., *Corylus avellana* L., *Fagus sylvatica*, *Fraxinus excelsior* L., *Sambucus nigra* L., *Quercus petraea* LIEBL. and *Ulmus glabra* HUDS.). Photosynthetically active radiation (PAR) was very low at this site thoughout the investigation period (Fig. 2).

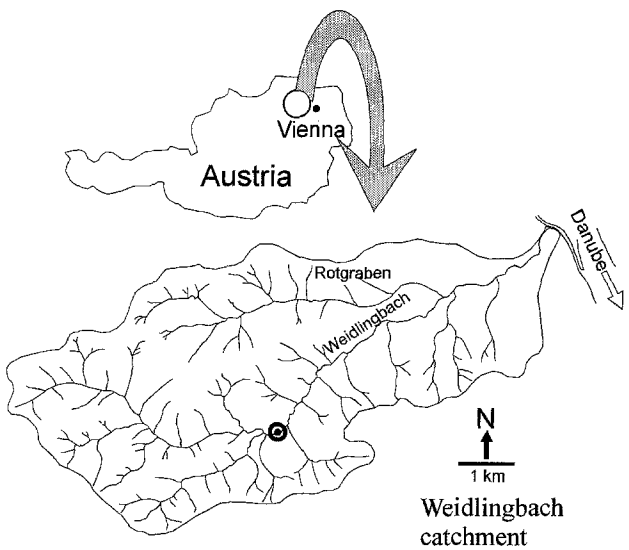

Fig. 1. The Weidlingbach catchment near Vienna, Austria. The study location is indicated by a dot.

The sunny site 2 was 22.3 m long and 13.3–13.7 m wide with bank inclinations ranging from 28° (right bank) to 50° (left bank). Because of sporadically growing bank vegetation (*Corylus avellana, Fagus sylvatica, Fraxinus excelsior, Sambucus nigra, Carpinus betulus* L., *Salix* spp.), PAR values were significantly higher (Fig. 2). The hinterland at both sites consisted of meadows (left bank) or mixed deciduous forest (right bank). Sediments are composed of coarse gravel (ARTMANN 2000).

Material and Methods

Abiotic variables

On each sampling date, PAR was measured midstream at the shady and sunny site (Skye Instruments).Water level fluctuations were obtained by an automatic gauging station situated approximately 500 m downstream of the study area. In addition, water temperature was measured using permanently exposed minimax thermometers.

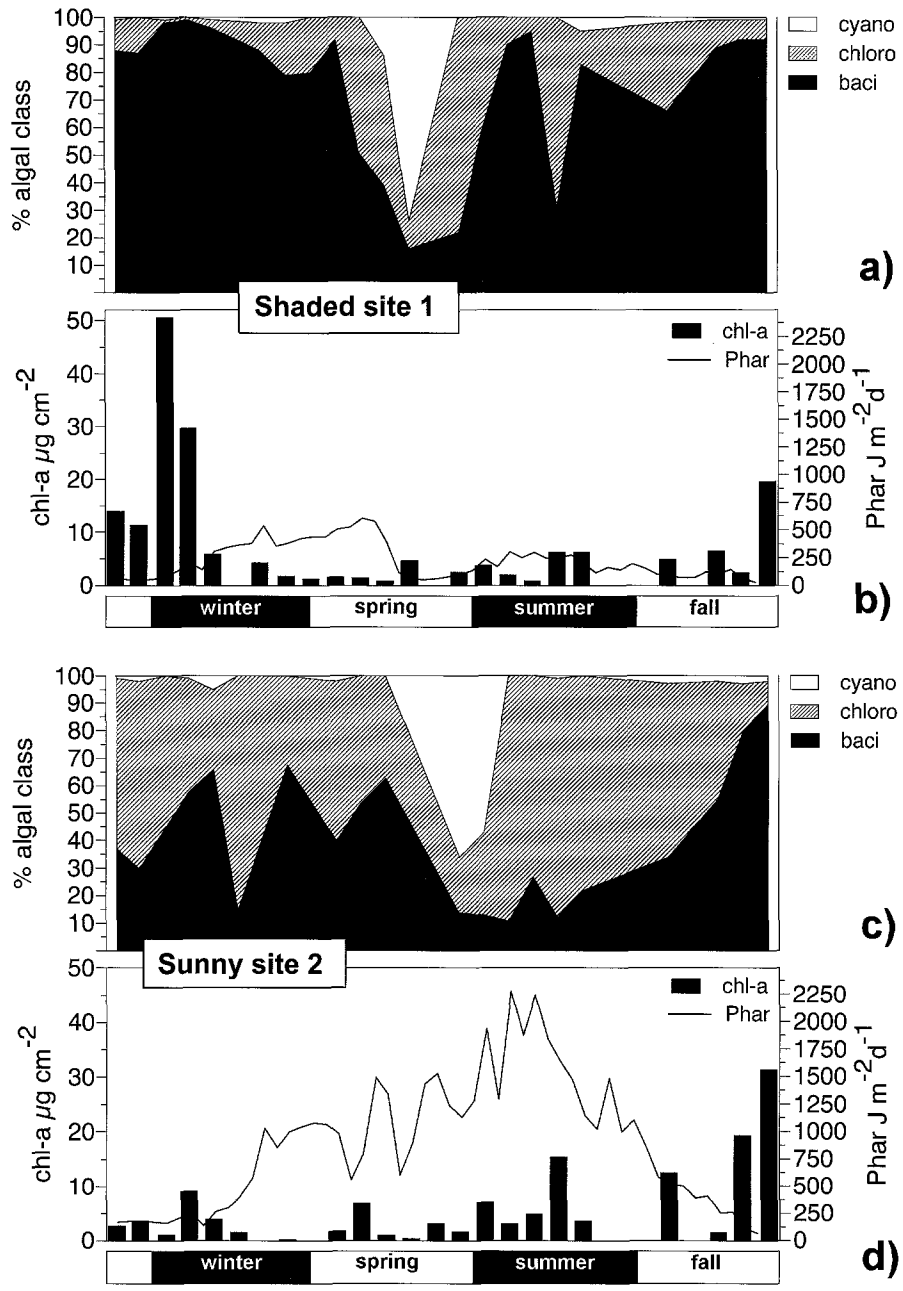

Fig. 2. Percentage of benthic algal classes (**a**) and total chlorophyll-a of phytobenthos on coarse gravel substrate (**b**) at the shaded site 1 and the sunny site 2 (**c**, **d**), respectively. Data range from December 1997 to December 1998. PAR is indicated by a solid line.

Algal biomass

Benthic algal biomass was measured from December 1997 to December 1998 in bi-weekly intervals (= 27 sampling dates). At each date, large pebbles (grain size = 50–60 mm) were chosen following the principles of random stratified sampling. Algae were collected using a modified Douglas sampler (DOUGLAS 1958). The funnel of the sampler was pressed against the upper substrate surface and benthic algae were completely removed by a fine wire brush (area sampled: 15.9 cm^2). Finally, the algal suspension was quantitatively collected by a suction apparatus and transferred to the laboratory. Six replicates were taken at each sampling date. To gain insight into community structure, periphyton was scraped off from gravel originating from morphologically different sections of each location (riffle, pool, banks, midstream).

In the laboratory, the algal suspension of a given sample was sub-sampled and filtered on preweighed and precombusted glass fiber filters (Whatman-GF/F). After drying (24 h, 95 °C) and reweighing, dry mass (DM) and ash mass (AM; 2–3 h, 550 °C) were determined. Ash-free dry mass (AFDM) was calculated by subtracting AM from DM. To compare autochthonous standing crop and allochthonous input, sterile pebbles were exposed at both sites. Sampling was done every two weeks as explained above. For the comparison, algal DM was calculated from chl-a; a content of 2% chl-a per unit DM was assumed.

For pigment analyses, a sub-sample of the suspension was filtered on glass fiber filters (Whatman GF/C) and stored at –20 °C (storage period between 1 and 14 days). Pigments were extracted by grinding the filters in 90% cold acetone, following an extraction at +2 °C for 12 h. Extraction steps were done under dim light conditions to minimize artefacts. The suspension was then centrifuged (2500 rpm, Juoan MR22) and the supernatant analyzed by means of HPLC according to WRIGHT et al. (1991; Merck-Hitachi HPLC system; ternary low pressure gradient with methanol, ethyl acetate and acetonitril; immediately before separation samples were diluted with distilled water; column: Merck-Superspher RP-18 250/4, precolumn: Merck-Lichrospher RP-8 endcapped). Peak detection and integration was done at 440 nm (SCHAGERL 1993; SCHAGERL et al. 1996; JEFFREY et al. 1997).

Percentages of individual algal classes were determined by calculating their respective chlorophyll-a (chl-a) part of the total chl-a using class-specific pigment ratios (Bacillariophyceae including Chrysophyceae: fucoxanthin; Cyanobacteria: echinenone; Chlorophyta: chl-b). The remaining extract was spectrophotometrically analysed (LKB 4053) following the procedure of JEFFREY & HUMPHREY (1975).

For microscopical work, a Reichert Polyvar supplied with differential interference contrast optics was used. For diatom determinations, combusted samples were embedded in Naphrax following the Naphrax manual. Subsamples of qualitative algal samples were analysed and identified both unpreserved and after preservation with Pfeiffer solution (BRAUNE et al. 1982).

Allochthonous input

CPOM collection followed algal biomass sampling with the exception of the main defoliation period, when the traps were emptied at weekly intervals. At each station aerial CPOM input was measured by two sets of permanently installed sampling units. Each set consisted of wooden frames (sampling area = 0.25 m^2) fastened to a twin rope stretched along a cross-section of the stream approximately 1.5 m above the mean water level. Around the upper fringe of each frame a collar of wire screen was fixed (0.1 m high); the bottom of each frame was covered by nylon net (mesh size: 1 mm) for drainage of rain water (WEIGELHOFER & WARINGER 1994). The number of frames depended on stream width; at site 1, three frames and at site 2 four frames were installed per sampling unit. Tests with marked leaves indicated that no loss of CPOM occurred even on extremely windy days.

Lateral input of CPOM was measured by exposing two tube traps on both the left and right banks. Each trap consisted of a plastic tube (length: 0.5 m, diameter: 0.1 m) which was split longitudinally, yielding an opening 3 cm wide. The tubes were fixed by steel bolts parallel to the water's edge 1 m above the mean water level (MOSER 1992). A steel plate attached to the slit opening provided access for particle input from the banks. Tube ends were closed by removable nets (mesh size: 1 mm) for drainage and sample removal. The samples were transferred in plastic bags to the laboratory, where the material was hand-sorted and divided into three categories: leaf litter, woody and miscellaneous particles (seeds, fruits, blossoms, etc.). Each CPOM category was dried at 95 °C for DM determination.

Organic matter retention

In order to investigate the CPOM retention capacity of the stream at the study sites, 300 leaves marked by coloured dots were uniformely released along a cross section upstream of each sampling station during base flow conditions. Leaves not trapped by woody debris or coarse sediment particles were caught by a net (mesh size: 1 cm) stretched across the stream downstream of each sampling station, yielding a maximum potential drift distance of 40 m at both sites. Two hours after release, leaf positions were mapped individually and leaves caught by the net were counted.

Results

Species composition

A total of 41 algal taxa was collected, belonging to the Bacillariophyceae (33), Cyanobacteria (4), Chlorophyta (2), Rhodophyta (1) and Chrysophyceae (1) (Table 1). At both sampling sites, diatoms dominated throughout the investigation period. At the shaded site 1, *Achnanthes minutissima* and *Amphora pediculus* were most abundant, whereas *Cocconeis pediculus* and *C. placentula* dominated at the sunny site 2. *Diatoma vulgaris, Gomphonema olivaceum, Navicula menisculus, N. lanceolata* and *N. tripunctata*, among others, were abundant at both sites. Furthermore, the rhodophyte *Chantransia* sp.was frequently observed at the shaded site and the chlorophyte *Cladophora glomerata* showed high abundance at the sunny site, peaking in summertime.

Abundance of algal classes and chl-a

Based on HPLC analyses, Bacillariophyceae, Chlorophyta and Cyanobacteria were the most abundant algal groups throughout the study period (Fig. 2). The two sampling sites showed distinct differences in the proportion of diatoms and chlorophytes. Whereas diatoms clearly dominated the phytobenthos assemblage at the shaded site, chlorophytes gained in importance at the sunny site. Cyanobacteria were abundant only in late spring and early summer and made up ≤ 5% during the remaining time of the year.

Mean annual chl-a was 8.65 μg cm^{-2} at the shaded site and 7.53 μg cm^{-2} at the sunny station. These differences were not significant (X^2 test; $P > 0.05$). At both sites, chl-a values were lowest in spring and summer (minimum= 0.002 g m^{-2} in March) and increased significantly ($P < 0.001$) to maximum amounts in late fall and early winter (0.507 g m^{-2} at the shaded station).

A high correlation was detected between AFDM and chl-a (Fig. 3), indicating a significant contribution of attached algae to the benthic community. At the shaded site, the coefficient of determination (r^2) was 0.61, at the sunny station 0.86.

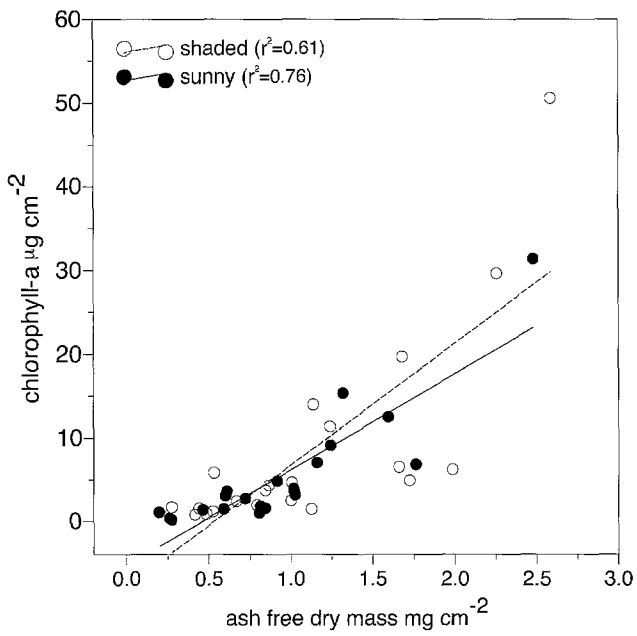

Fig. 3. Correlation between ash-free dry mass (mg cm^{-2}) and chlorophyll-a (μg cm^{-2}) of phytobenthos on coarse gravel substrate at the shaded site 1 (black dots, solid regression line) and the sunny site 2 (open circles, broken regression line).

Gravimetric variables of phytobenthos

At the shaded site, algal DM ranged from 13 g m^{-2} in April to 440 g m^{-2} in August (annual mean = 93 g m^{-2}; Fig. 4a) and at the sunny site from 3 g m^{-2} in May to 512 g m^{-2} in late fall (annual mean = 70 g m^{-2}; Fig. 4c). These differences were not significant (X^2 test; $P > 0.05$). Proportions of AFDM on DM ranged from 10 to 100%, with higher percentages observed during spring and summer (Figs. 4b, d).

Allochthonous CPOM input

At the shaded site with its dense tree canopy, total annual aerial input was 665 g DM m^{-2}, at the sunny location 382 g DM m^{-2}. The most important fraction of direct input was leaf litter which contributed up to 75–77% of total allochthonous CPOM. The fraction of wood and miscellaneous particles ranged from 2–16% and 9–21%, respectively.

Direct CPOM input was significantly highest (X^2-test; $P < 0.05$) during the period of defoliation from October to November. In the course of this period, 61.1% (shaded) to 64.9% (sunny) of the annual CPOM dropped into the stream, yielding daily input rates of 6.6 to 4.0 g DM m^{-2}. From December to September, daily direct input rates decreased to 0.84 g DM m^{-2} (shaded) and 0.44 g DM m^{-2} (sunny). By dividing into different fractions, 66–97% of the direct CPOM input could be traced back to leaf litter that fell during October and November. Input of boughs and branches showed no distinct pattern; some peaks were observed in winter and spring due to intense rainshowers and stormy weather. Peaks in the miscellaneous particle fraction were heavily influenced by blossom periods and seedfall of the riparian vegetation. Along the cross-sections of the stream, no spatial distribution patterns of direct CPOM input could be detected.

Table 1. Species inventory of phytobenthic taxa at the Weidlingbach. Abundance classes 1 to 3 are estimates of the proportion of species present at the shady site 1 and the sunny study site 2 (1 – rare, 2 – medium, 3 – high abundance).

Taxon	Shady site 1	Sunny site 2
CYANOBACTERIA		
Chroococcus sp.	–	1
Oscillatoria sp.	2	2
Phormidium foveolarum Gom. 1892	1	2
Pseudanabaena catenata Lauterborn	2	1
HETEROKONTOPHYTA		
Bacillariophyceae		
Achnanthes lanceolata (Brebisson) Grunow in Cleve & Grunow 1880	2	2
Achnanthes minutissima Kützing 1883	3	2
Amphora ovalis Kützing 1844	1	1
Amphora pediculus (Kützing) Grunow 1880	3	2
Cocconeis pediculus Ehrenberg 1838	2	3
Cocconeis placentula Ehrenberg 1838	2	3
Cymatopleura elliptica (Brebisson) W. Smith 1851	2	1
Cymatopleura solea (Brebisson) W. Smith 1852	1	2
Cymbella affinis Kützing 1844	1	1
Cymbella minuta Hilse ex Rabenhorst 1862	1	1
Diatoma ehrenbergii Kützing 1844	1	2
Diatoma moniliformis Kützing 1833	2	2
Diatoma vulgaris Bory 1824	3	3
Diploneis elliptica (Naegeli) Cleve-Euler 1922	1	–
Fragilaria ulna (Nitzsch) Lange-Bertalot 1980	1	1
Gomphonema angustum Agardh 1831	2	1
Gomphonema olivaceum (Hornemann) Brebisson 1838	3	3
Gomphonema parvulum (Kützing) Kützing1849	1	1
Gomphonema tergestinum Fricke 1902	2	2
Gyrosigma attenuatum (Kützing) Rabenhorst 1853	1	1
Gyrosigma scalproides (Rabenhorst) Cleve 1849	–	1
Melosira varians Agardh 1827	1	2
Navicula capitatoradiata F. Germain 1981	2	1
Navicula lanceolata (Agardh) Ehrenberg 1838	3	3
Navicula menisculus Schumann 1867	3	3
Navicula tripunctata (O.F. Müller) Bory 1822	3	3
Nitzschia acicularis (Kützing) W. Smith 1853	1	1
Nitzschia angustata (W. Smith) Grunow 1853	1	1
Nitzschia dissipata (Kützing) Grunow1862	3	3
Nitzschia linearis (Agardh) W. Smith 1853	1	1
Nitzschia sigmoidea (Nitzsch) W. Smith 1853	2	2
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot 1980	3	3
Surirella brebissonii Krammer & Lange-Bertalot 1987	2	2
Chrysophyceae		
Phaeodermatium rivulare Hansgirg 1889	1	1
CHLOROPHYTA		
Cladophora glomerata (L.) Kützing	2	3
Ulothrix tenuissima Kützing	1	–
RHODOPHYTA		
Chantransia sp. Bory de St. Vincent 1823	3	1

Annual riparian CPOM input varied between 1006 g DM m^{-1} of stream length at the shaded station and 1062 g DM m^{-1} at the sunny site. Within the same station, lateral input rose with increasing bank inclination; no significant differences were observed at different sites with comparable inclinations. Within the lateral input pathway, leaf litter was the most important fraction, yielding 74–80% of total CPOM input, whereas wood accounted for 9–16% and miscellaneous particles for 10–11%. At the shaded site, annual CPOM input was up to 774 g DM m^{-2} a^{-1}; 86% of this amount was due to aerial and 14% to riparian input. At the sunny station, total input was 460 g DM m^{-2} a^{-1} (83% aerial, 17% riparian).

Autochthonous algal biomass *versus* allochthonous CPOM input

The seasonal patterns of algal biomass (based on chl-a) and CPOM input at both sampling locations are shown in Fig. 5. At both sites and within all seasons, total CPOM

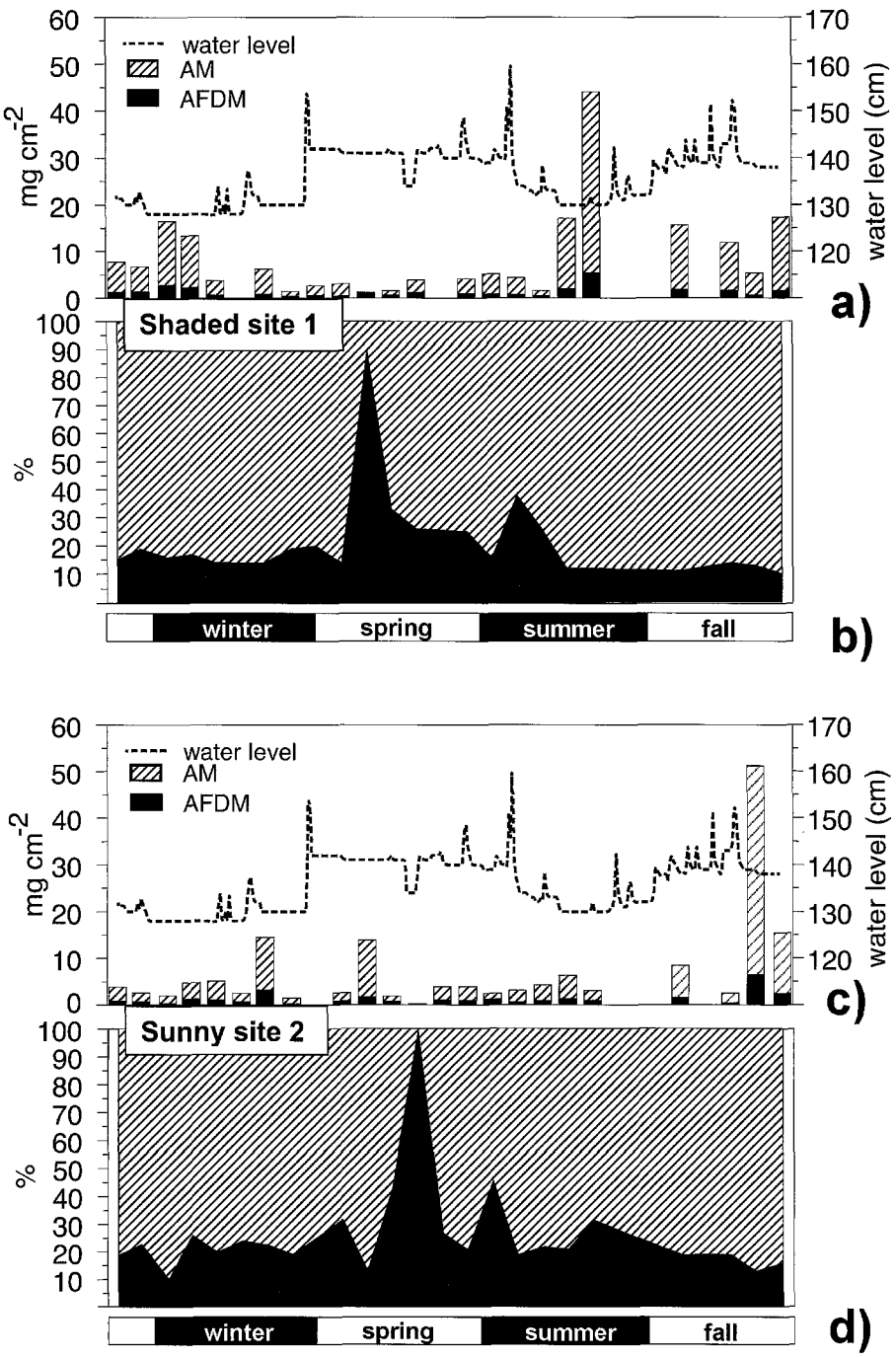

Fig. 4. Ash mass (AM) and ash-free dry mass (AFDM) (**a**) and the proportion of AM and AFDM of phytobenthos on coarse gravel substrate (**b**) at the shaded site 1 and the sunny site 2 (**c**, **d**), respectively. Data range from December 1997 to December 1998. In Figures a and c, the water level is indicated by a broken line.

input was very highly significantly (X^2 test; $P < 0.001$) higher than autochthonous algal biomass. At the shaded site 1, algal biomass was highest in summer (2.6 g DM m^{-2}) and lowest in winter (1.0 g DM m^{-2}); at the sunny site 2 an opposite pattern was observed, with algal biomass peaking in winter (winter: 2.5 g DM m^{-2}; autumn: 0.6 g DM m^{-2}). Allochthonous input (lateral + aerial input) was generally highest in autumn and lowest in winter (shaded site: 454.6 g DM m^{-2} *versus* 86.5 g DM m^{-2}; sunny site: 348.6 g DM m^{-2} *versus* 21.4 g DM m^{-2}, Fig. 5).

Retention capacity

At both sites, the relationship between CPOM drift distance (x) and the percentage of marked leaves trapped by the sediment surface (y) was well described by a modified exponential decay law. For site 1 (shady site) the regression equation was $y = 31.98 + \exp(4.21–0.086x)$, for site 2 (sunny site) $y = 36.33 + \exp(4.09–0.104x)$; the coefficient of determination (r^2) was ≥ 0.98 in both cases (Fig. 6). The regressions were not significantly different (t-test; $P > 0.05$). A proportion of 70% of the total (= 300 leaves) was retained within 40 m, and 50% within 16 m from the release point. However, at the shady site 1 the transport was smoother than at the sunny site 2, reflecting an even distribution of coarse sediment particles throughout the 40 m reach. At site 2, on the other hand, 21% of the total was retained by an accumulation of cobbles and boulders within the first 2 m, and restricted transport was observed until 10 m from the release point. From 22 to 32 m from the release point, retention capacity was distinctly reduced (Fig. 6).

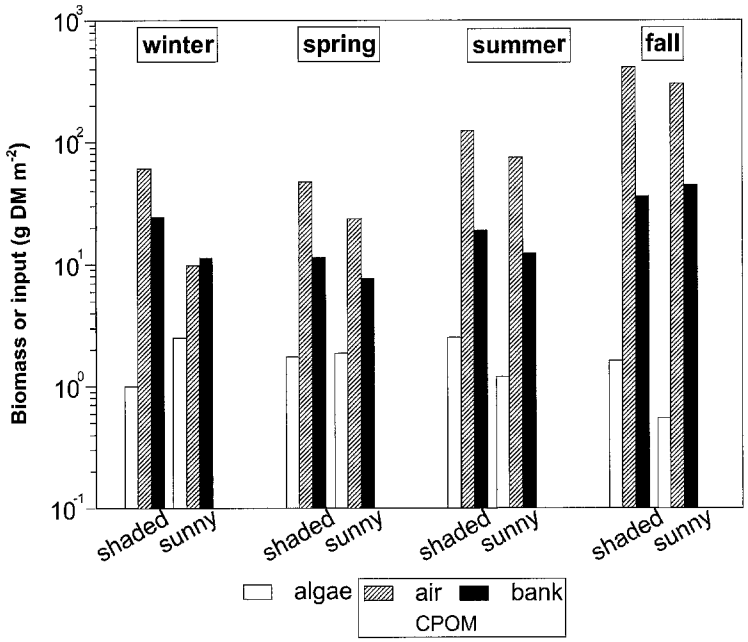

Fig. 5. Seasonal allochthonous input (g dry mass m^{-2}) of coarse particulate organic matter [CPOM; aerial (= air) and lateral input (= bank)] and autochthonous phytobenthic biomass based on chl-a (algae) at the shaded site 1 and the sunny site 2.

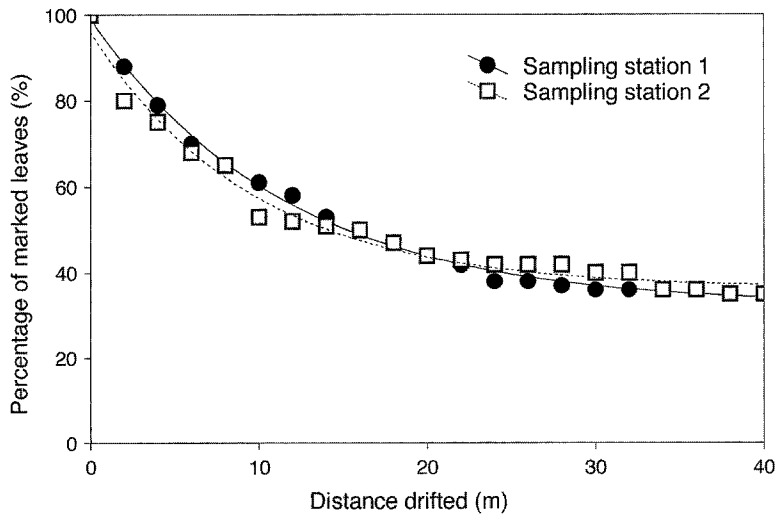

Fig. 6. CPOM retention at the shaded and sunny sampling station, illustrated by the percentage of marked leaves (n = 300 per station) trapped by the sediment surface at a given distance from the release point. Data for the not significantly different ($P > 0.05$) regression lines are given in the text.

Discussion

Autochthonous input

Benthic algae represent successful and important primary producers in streams (BIGGS 1996; STEVENSON 1996), yielding AFDM values up to 11 mg cm^{-2} and chl-a values up to 56.6 µg cm^{-2} (Table 2). Among the multitude of abiotic (e.g. hydrology, substrate, water and nutrient chemistry, water temperature) and biotic determinants (herbivory, parasitism, allelopathy, competition) (TETT et al. 1978; ROTT & PFISTER 1988; BIGGS & GERBEAUX 1993; PFISTER 1994; PETERSON & STEVENSON 1993; BURKHOLDER 1996; MCCORMICK 1996; STEVENSON 1997; FAYOLLE et al. 1998; SHERWOOD & SHEATH 1999), light is undoubtedly the most important *factor limitans* of benthic algal growth in shaded stream sections (STEINMANN & MC INTYRE 1986; DUNCAN & BLINN 1989; HILL & HARVEY 1990; BENFIELD et al. 1991; HEPINSTALL & FULLER 1994; HILL 1996; DENICOLA & HOAGLAND 1996). This is even more valid in low order streams where the catchment and the banks are densely wooded by deciduous forest (HEPINSTALL & FULLER 1994; DENICOLA & HOAGLAND 1996; HILL 1996; KJELDSEN et al. 1998). At such locations, benthic algal biomass negatively correlates with canopy density of the riparian vegetation (HILL & HARVEY 1990). In the present study, this relationship was explicitly found in terms of chl-a (Fig. 2), which showed distinctly lowest amounts in spring and summer (minimum = 0.002 g m^{-2} in March), but highest values in late fall and winter (up to 0.507 g m^{-2}). These findings correspond well with data given by HEPINSTALL & FULLER (1994) for a low-order stream in New York. A spring peak of chl-a immediately before the onset of foliation, as has been observed by SHAMSUDIN & SLEIGH (1994) at the River Itchen (Southhampton) and in an Indian stream (ROUT & GAUR 1994), could not be detected in the present study, probably because of high-water events. Chl-a was positively correlated with PAR at the sunny site during summer, but did not reach its maximum before defoliation in late autumn. Other ecological factors like algal competition, succession state and macrozoobenthic grazing might also have modified the relationship between PAR and chl-a at the sunny site.

Another important aspect is the observation that the species inventory changes when comparing unshaded and shaded streams or stream sections (HILL & KNIGHT 1988; HILL & HARVEY 1990; HILL 1996); at high light intensities, Chlorophyta and Cyanobacteria are favoured, whereas Bacillariophyta are much more abundant at low light intensities with Chlorophyta and Cyanobacteria strongly decreasing (DUNCAN & BLINN 1989). As algal biomass is heavily influenced by species composition (STEINMANN & MCINTYRE 1986; SHAMSUDIN & SLEIGH 1994; ROUT & GAUR 1994; FAYOLLE et al. 1998; MOSISCH et al. 2001), this reciprocal taxa shift might explain why the differences in mean annual algal DM were not significantly different at our sunny and shady location.

Comparisons between periphyton dry mass and CPOM (DM) standing stock at the study site may be made by using data given by WEIGELHOFER & WARINGER (1999). Based on 120 samples made over one year with an Hess sampler, the mean standing stock of CPOM (DM) on the sediment surface of the Weidlingbach study site ranged from 60 g m^{-2} to 340 g m^{-2} (mean ± SD = 115.0 ± 70.0 g m^{-2}) (WEIGELHOFER & WARINGER 1999). In debris dams, however, retained CPOM dry mass was much higher, ranging up to 22 kg m^{-2}. On average, one debris dam per 35 m stream length was present at the study site (WEIGELHOFER & WARINGER 1999), being equivalent to a DM of approximately 63 g CPOM m^{-2}. Based on these data, CPOM standing stock at the study site averaged 178 g DM m^{-2} and was very highly significantly ($P < 0.001$) higher than periphyton dry mass at both sites which made up 52% of CPOM standing stock at the shaded site and 39% at the sunny site.

Besides light, substrate type plays an important role for benthic algal growth (TETT et al. 1978; SOBCZAK & BURTON 1996). Among the multitude of phytobenthic substrates (cobbles, pebbles, gravel, sand, mud, submerged wood, macrophytes) (SCHÖNBORN 1996; SABATER et al. 1998), stones with favourable orientation towards the current are especially important because they represent stable elements in running waters (ROTT & PFISTER 1988; BORCHARDT & BOTT 1995; CAZAUBON et al. 1995; BIGGS 1996; BURKHOLDER 1996; SABATER & ROMANI 1996; VALETT et al. 1996; SCHAGERL & DONA-

Table 2. Summary of biomass parameters [chl-a (µg cm^{-2}) and/or ash-free dry weight (AFDW; mg cm^{-2})] of benthic algae on natural substrates in streams.

Chl-a (µg cm^{-2})	AFDW (mg cm^{-2})	Reference
–	0.01–11	BACKHAUS (1968)
0.0–56.6	0.0–4.7	BIGGS & GERBEAUX (1993)
1.0–2.5	2.0–5.0	BIGGS & HICKEY (1994)
2.3–86	–	BOSTON & HILL (1991)
0.1–1.2	–	CATTANEO & ROBERGE (1991)
0.001–0.15	–	CATTANEO et al. (1997)
0.1–13.8	–	DAVIES & GEE (1993)
0.05–0.31	–	KJELDSEN et al. (1998)
–	< 0.4	PFISTER (1994)
0.9–2.3	0.3–0.6	ROSEMOND (1994)
0.1–40.6	0.1–7.1	SCHAGERL & DONABAUM (1998)
0.2–41.5	–	SHAMSUDIN & SLEIGH (1994)
0.01–0.18	–	TETT et al. (1978)
0.2–50.7	0.06–5.4	this paper

BAUM 1998). Coarse substratum is mainly chosen by filamentous algae, wheras fine sediment is frequently favoured by mobile diatom species (e.g. *Navicula* spp.). However, scouring by suspended particles and ice as well as hydraulic stress during high discharge strongly affect phytobenthic communities even on stable substrates (BACKHAUS 1968; TETT et al. 1978; ROTT & PFISTER 1988; ACS & KISS 1993; PADISAK 1993; HEPINSTALL & FULLER 1994; ROSEMOND 1994; BIGGS 1996; PETERSON 1996). In the present study, the impact of spring spates was almost negligible in fast-growing Bacillariophyceae, but heavily affected filamentous algae, e.g. slowly-growing Cyanobacteria and the chlorophyte *Cladophora glomerata*. The latter colonized up to 30% of the sunny site, but, due to the heavy flood effects in this area, the annual mean of DM was lower than that of the shady site (70 g m^{-2} *versus* 93 g m^{-2}). Similar detrimental effects on filamentous algae during floods were observed by UEHLINGER (1991) and HORNER et al. (1990); with increasing discharge the latter authors recorded a shift from filamentous algae (e.g. *Phormidium* sp., *Mougeotia* sp.) to diatom species (*Fragilaria* sp., *Synedra* sp.). Under such conditions many diatom taxa benefit from their attachment mechanisms. In the present study, the frequent occurrence of *Achnanthes lanceolata*, *A. minutissima* and *Cocconeis placentula* could be traced back to the close attachment to the substrate. Floods, however, may also positively affect phytobenthic diversity following the principles of the intermediate disturbance hypothesis, thereby creating a balance between the autotrophic and heterotrophic compartment (FAYOLLE et al. 1998).

Allochthonous input

In their comprehensive investigation, FISHER & LIKENS (1973) pointed out that allochthonous organic matter input originating from the riparian vegetation was the main energy source of the rivulet Bear Brook (New Hampshire). Since this fundamental study, the importance of CPOM for stream ecosystems has been demonstrated frequently (VANNOTE et al. 1980; CUMMINS et al. 1983; CUSHING 1988; SMOCK 1990; GAZZERA et al. 1991; CAMPBELL et al. 1992; BILBY & BISSON 1992; BASAGUREN et al. 1996; WALLACE & WEBSTER 1996; ABELHO & GRAÇA 1998; SIMON & BENFIELD 2001). Annual CPOM input data for selected streams are shown in Table 3. In European streams and rivers, annual aerial input of CPOM ranges from 42 g DM m^{-2} to 1719 g m^{-2}, with mean values of 530 g m^{-2} (WEIGELHOFER & WARINGER 1994). This value is close to the observed mean annual input of the Weidlingbach (523 g m^{-2}; range: 382 g $m^{-2}a^{-1}$ at the sunny site – 665 g $m^{-2}a^{-1}$ at the shady location) and also close to the mean value of 450 g m^{-2} commonly found in temperate climates (BRAY & GORHAM 1964).

Generally, catchments with deciduous forest in northern temperate latitudes yield maximum direct CPOM input during defoliation in autumn (MOSER 1992; RICHARDSON 1992; WEIGELHOFER & WARINGER 1994; BENFIELD 1997; POZO et al. 1997; ABELHO & GRAÇA 1998). This pattern was observed in the Weidlingbach as well: more than half of the annual CPOM input (with 95% belonging to the leaf fraction) occurred in autumn. A small secondary peak of aerial CPOM input appeared

Table 3. Annual CPOM input for selected streams and rivers. Input is divided into bank, aerial and total input (g DM).

Bank input g DM m^{-1} a^{-1}	Aerial input g DM m^{-2} a^{-1}	Total input g DM m^{-1} a^{-1}	Reference
–	–	715	ABELHO & GRAÇA (1998)
–	–	243.3	BÄRLOCHER (1983)
7.6–17.2	18.3–260.3	57.3–893.6	BILBY & BISSON (1992)
–	–	61–617	CAMPBELL et al. (1992)
31.1–64.4	17.8–466.7	255.6–1048	CONNERS & NAIMAN (1984)
12.6–49.6	27–231	48.4–477.8	CUSHING (1988)
5.9–409.9	111.4–396.3	125–3150	GURTZ et al. (1988)
–	–	273.2–285.2	HILL & BROOK (1996)
–	–	389	KILLINGBECK & WALI (1978)
98.8–1858.5	117.6–203	2619.6–4021	MOSER (1992)
–	–	511.8–751.4	POZO et al. (1997)
–	234–516	–	RICHARDSON (1992)
–	585.6–1067	–	SMOCK (1990)
46.6–594.9	362–716	–	WEIGELHOFER & WARINGER (1994)
1006.2–1061.5	381.5–664.9	–	this paper

in spring, consisting mainly of fruits and seeds, an observation also made by SMOCK (1990), WEIGELHOFER & WARINGER (1994), HILL & BROOKS (1996) and ABELHO & GRAÇA (1998).

Differences in direct CPOM input largely depend on stream size and the extent of canopy closure. According to CONNERS & NAIMAN (1984), annual direct CPOM input is negatively correlated with stream order. However, stream order is frequently only of limited value as a parameter when comparing input data from different running waters. For example, direct input at the fourth order station at the Mauerbach near Vienna (stream width = 4.2 m) was three to five times higher than at the Oberer Seebach at Lunz, a second order mountain stream 17.5 m wide (WEIGELHOFER & WARINGER 1994). With increasing stream width, the canopy of forested streams commonly opens midstream. Therefore, direct input decreases in the center of a given cross-section (CONNERS & NAIMAN 1984; MOSER 1992), reducing net input per square metre. Apart from stream width, direct CPOM input is also heavily influenced by species composition and density of the riparian vegetation. This has been thoroughly demonstrated at study sites where these parameters changed rapidly in space or time (CUSHING 1988; GURTZ et al. 1988; CAMPBELL et al. 1992; POZO et al. 1997; WEBSTER & MEYER 1997). Data of the present study support the combined effects of stream width and canopy closure. The shaded station with a canopy closure around 100% showed high aerial input with no decrease along the cross-section baskets, whereas at the broader sunny site with only 20% canopy closure a reduced overall CPOM input with a midstream depression was observed.

According to the literature, the magnitude of annual lateral CPOM input depends upon bank inclination (CUSHING 1988; MOSER 1992; WEIGELHOFER & WARINGER 1994), density and composition of the riparian vegetation (CUSHING 1988; GURTZ et al. 1988; MOSER 1992) and upon meteorological variables (CUSHING 1988). In the present study, the proportion of bank input in total CPOM input increased with decreasing canopy closure. Additionally, we observed a distinct correlation between bank inclination and bank CPOM input. Lateral input data of different streams are often difficult to compare due to missing information on the accompanying variables used. For the Oberer Seebach at Lunz (Table 3; MOSER 1992) and the Mauerbach near Vienna (Table 3; WEIGELHOFER & WARINGER 1994) input data range from 46.6 (bank slope 18°) to 1858.5 (slope 41°) g DW m^{-1} particulate organic matter > 0.5 µm. Lateral input rates of the Weidlingbach were generally higher than those of American and Australian brooks included in Table 3 because of the steep banks, the dense riparian vegetation and the scarce understory in the riparian zone of this brook. Lateral input often displays two main input periods, one in October/November corresponding to autumnal leaf fall and a second, smaller one in spring (CONNERS & NAIMAN 1984; MOSER 1992). Both peaks were observed at the Weidlingbach, too. Between September and November, 52–59% of annual lateral input was detected, consisting mainly of shed leaves (82–93%). The spring peak displayed a strong component of wood deposits and was most likely due to the rains common in this season. In contrast to direct input, the autumnal peak of lateral input is less distinct and often prolonged into the winter months (WEBSTER et al. 1990; MOSER 1992), providing the stream biota with an additional food source during a time of generally low input.

At streams with uniform canopy, aerial CPOM input per metre stream length increases with stream width. As the absolute amount of lateral input is independent of stream size, the proportion of the input from the banks naturally declines when the stream broadens. In some studies, lateral input constitutes about 10 to 64% of total CPOM input (FISHER & LIKENS 1973; CONNERS & NAIMAN 1984; GURTZ et al. 1988; WEBSTER et al. 1990; BILBY & BISSON 1992; BENFIELD 1997; WEBSTER & MEYER 1997). At the Weidlingbach, the portion attributable to lateral input was 14% at the shady and 17% at the sunny location. It can be concluded that lateral input plays an important role in total CPOM input in low order streams and therefore must not be neglected in estimating annual energy budgets.

The stream biota's ability to process and use CPOM depends primarily on the retention capacity of a given stream section (BILBY & LIKENS 1980; SMOCK et al. 1989; HILDREW et al. 1991; WEBSTER et al. 1994; CANHOTO & GRAÇA 1998; JACOBSON & JACOBSON 1999). Besides sediment structure and debris dams, discharge has been frequently identified as a determinant for retention capacity (SPEAKER et al. 1984; TROTTER 1990; JONES & SMOCK 1991; EHRMAN & LAMBERTI 1992). Generally, due to the low base flow of low order streams, retention is greatly enhanced compared with larger rivers (NAIMAN et al. 1987; PROCHAZKA et al. 1991; MINSHALL et al. 1992). Our results support this observation: at the third order study sites and during base flow, about 70% of marked leaves were recovered by sediment particles within 40 metres of the release point, underlining the intact channel morphology of the study sites. As CPOM retention and export (= 30% of marked leaves) were not significantly different ($P > 0.05$) at two consecutive sampling sites within the same stream section, we conclude that CPOM drift import approximately equals CPOM drift export at the Weidlingbach section studied. The findings from the Weidlingbach are in the range of data given by SPEAKER et al. (1984), PROCHAZKA et al. (1991) and CANHOTO & GRAÇA (1998), who reported 90% of the leaves being recovered within a 10–81 m long stretch of stream bed. Further processing of retained material

involves both microbial and fungal colonization as well as transformation by mechanical breakdown and shredder activity (COVICH & CROWL 1990; EHRMANN & LAMBERTI 1992; CUSHING et al. 1993; ROBINSON et al. 1998; GRAÇA et al. 2001).

Summary

At our study sites, algal biomass ranged from 0.6–2.6 g DM m^{-2}. Allochthonous input (lateral + aerial input) was generally highest in autumn and lowest in winter (shaded: 454.6 g DM m^{-2} *versus* 86.5 g DM m^{-2}; sunny: 348.6 g DM m^{-2} *versus* 21.4 g DM m^{-2}) with aerial input being a more important pathway for CPOM than riparian input. When comparing total CPOM input with CPOM standing stock per m^2 (WEIGELHOFER & WARINGER 1999), the percentage of the latter is roughly equivalent to 32% of total annual CPOM input, suggesting a CPOM turnover rate of 3–4 months in the Weidlingbach stream section studied. As up to two thirds of CPOM input is retained within 40 metres of the input location we conclude that CPOM drift plays only a minor role in CPOM replenishment of the study stream, and that the CPOM turnover at a given stream section is fed mostly by aerial input.

Acknowledgements

We wish to thank Michael Stachowitsch for correcting the English text.

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